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The importance of termites (Isoptera) for the recycling of herbivore dung in tropical ecosystems: a review

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Abstract. While the key role of termites in the decomposition of litter in the tropics has been acknowledged for a long time, much less information exists on their importance in the recycling of dung of primary consumers, especially herbivores. A review of published studies shows that a diverse group of termites (at least 126 species) has been reported to feed on a wide range of mammalian dung (18 species). Predominantly, wood-feeding and polyphagous wood-litter feeding species were found to feed also frequently on dung. Moreover, we found that termites can quickly remove large amounts of mammalian dung, especially in the dry season, when on average about 1/3 of the dung deposited in a given habitat is removed by termites within one month (with the highest rates observed in savannas). No distinctive preference for mammalian dung over other organic food sources was observed for fungus-growing termites (Macrotermitinae), whereas the majority of the non-fungus growing taxa studied prefer dung over other food. As termites bring large quantities of dung below the soil surface, disturb and enrich soils with nutrients, dung feeding by termites appears to be a previously underestimated process important in the functioning of tropical ecosystems.

INTRODUCTION

Termites are widely distributed throughout the tropical and subtropical regions of the world, with the highest diversity found in tropical forests (Eggleton, 2000). By the early 1970's approximately 1900 living and fossil species of termites had been described (Lee & Wood, 1971) and a constant flow of first descriptions is still increasing this number significantly. Termites (taxon-dependent) act as herbivores as well as decomposers, feeding on a wide range of living, dead or decaying plant material (Adamson, 1943; Noirot & Noirot-Timothee, 1969; Lee & Wood, 1971; Wood, 1976, 1978; Bignell & Eggleton, 2000; Traniello & Leuthold, 2000), including the consumption and turnover of large volumes of soil rich in organic matter and fungi. These feeding habits make termites important ecosystem engineers, which over long periods of time can modify the physical properties of soil such as texture, water infiltration rates and nutrient content, at various spatial scales (e.g. Dangerfield et al., 1998).

Previous overviews of the food and feeding habits of termites either only list mammalian dung as just one possible food item (Lee & Wood, 1971; Wood, 1976, 1978; Bignell & Eggleton, 2000; Traniello & Leuthold, 2000) or even do not mention mammalian dung (Adamson, 1943; Noirot & Noirot-Timothee, 1969). Only one old paper focuses on the utilization of mammalian dung by termites (Ferrar & Watson, 1970), but it is restricted to data from the Australian region. It does not include the more recent work on the subject, and does not address the ecosystem consequences of dung feeding by termites

(Ferrar & Watson, 1970). The lack of studies on the role of termites as dung feeders is in strong contrast to the many on the role of dung beetles in the comminution and decomposition of herbivore dung, especially their importance in nutrient cycling (reviewed in Hanski & Cambefort, 1991). So far, the question to what extent and which species of termites consume mammalian dung and whether termites might fulfil a similar ecosystem role as dung beetles, has remained largely unanswered. In this paper we therefore review the existing literature on the processing of herbivore dung by termites, from both a termite autecological perspective, as well as its ecosystem consequences.

THE AUTECOLOGICAL PERSPECTIVE

Consumption of mammalian dung

We identified 24 studies, published between 1955 and 2004 that contain detailed data on the consumption of mammalian dung by termites (Appendix). These studies report in total 126 taxa of termites feeding on dung. This number represents a conservative count and is most likely an underestimate: studies reporting that a termite genus utilizes dung with no species specification were counted only once and omitted completely from the count if another publication provided a species-specific record for the same genus. Representatives of the families Mastotermitidae, Rhinotermitidae and predominantly Termitidae feed on dung. In our list the genus *Amitermes*, family Termitidae, is remarkable, in that at least 35 species are reported to use dung as a food source. This observation might be explained by the high diversity (Scheffrahn et

al., 1999) as well as the polyphagy and tropicopolitan distribution of this genus (Eggleton, 2000), which is most diverse in semi-arid habitats (Scheffrahn & Su, 1987).

The majority of the records were in surveys of termite diversity, a few field (using mostly cattle-dung/cattle-manure, exceptionally elephant dung) and one laboratory study, which provided only descriptive data (Skaife, 1955). There are reports of termites foraging for mammalian dung from around the globe: Africa, Asia, Australia and North-/Central-/South-America. Most observations were made in Australia and Africa, potentially mirroring a skewed emphasis on the feeding habits of termites living in grass- and bush-lands on these continents.

These studies reveal that termites feed on the dung of a total 18 mammalian species: black rhinoceros (*Diceros bicornis*), African buffalo (*Syncerus caffer*), cattle (*Bos taurus*), camel (*Camelus* sp.), dikdik (*Madoqua* sp.), donkey (*Equus asinus asinus*), African elephant (*Loxodonta africana*), goat (*Capra aegagrus hircus*), horse (*Equus caballus*), hyrax (Hyracoidea), impala (*Aepyceros melampus*), kudu (*Tragelaphus* sp.), kangaroo/wallaby (Macropodidae), sheep (*Ovis aries*), duiker (Cephalophinae), springbok (*Antidorcas marsupialis*), wombat (Vombatidae) and zebra (*Equus quagga* ssp). There are no references to a particular termite species feeding mainly on the dung of one particular mammalian herbivore species. An analysis of the collective records indicates that predominantly wood-feeding (42 species = 39%) as well as polyphagous wood-litter feeding termite species (27 = 25%) also feed on mammalian dung. In comparison, 17 litter (= 16%) and 22 (= 20%) soil-feeding termite species show the same behaviour. This consumption of mammalian dung by termites is of more than incidental importance. This provokes the question, how do termites manage to locate this food source which is spatially and temporally heterogeneously distributed?

Locating dung

Johnson & Whitford (1975) studied the foraging behaviour of unidentified subterranean termites in the Chihuahuan desert and found that *Yucca elata* logs and cattle dung, which have a large surface area in contact with the soil, were preferred over small twigs and surface litter. They conclude that the modified environment under a large object on the soil surface (e.g. increased moisture content) is a necessary factor in food suitability, at least for subterranean termites. Ettershank et al. (1980) used baits in the field to see if this modified environment is also used to locate the food. They conclude that desert subterranean termites locate relatively large objects on the surface, such as cattle dung and *Yucca* sp. logs, by sensing the thermal shadows cast by such items. However, is dung particularly attractive to termites from a nutritional perspective, or just an accumulation of organic matter?

Nutrition

As Higashi et al. (1992) outline, termites generally feed on dead plant material that has a carbon to nitrogen ratio much higher than their own tissues and have to balance

their C and N inputs. The same authors list two classes of such C-N balancing mechanisms: adding N to inputs or selectively eliminating C, both achieved with the aid of microbial symbionts. But the lower the C/N ratio of the diet, the less urgent this balancing. Matsumoto (1976) reports C/N ratios of 4 to 12 for termite tissues, whereas fresh dead wood has C/N ratios as high as 350 to 1000 (LaFage & Nutting, 1978). For comparison, Ouédraogo et al. (2004) provide data on the C/N ratio of the baits they presented to termites: *Andropogon* straw = 153 (0.32% N), cattle dung = 40 (0.95% N), maize straw = 59 (0.77% N). Thus, the cattle dung provided to the termites in this study has a much more favourable C/N ratio than the alternative food items and might, therefore, be attractive to termites. In spite of this, and the clearly high phosphorous levels in cattle dung (1.06% vs. 0.03% in *Andropogon* straw and 0.18% in maize straw), the soil macrofauna preferentially removed the straw (Table 2, later discussion). This may mean that the symbiotic opportunities available to termites to compensate for very low food quality simply overrule the need to be highly selective in terms of the C/N ratio of food. Despite the various biochemical processes involved, this may accordingly hold true for both – endo- and ectosymbiotic (fungus-growing) termites.

Alternatively, or additionally, the physical parameters bulk density, texture and spatial location of dung might make this food source attractive to termites. Compared to the alternatives, such as standing dead grass, dung pats are an easily available local accumulation of litter and organic matter, aggregated by large herbivores. Termites might simply benefit energetically by exploiting dung pats with a high mass per volume ratio, instead of feeding on grass litter that needs to be collected over a wider spatial range and in a more unfavourable microclimate. Moreover, the mammalian herbivores and their endosymbionts mechanically (fragmentation) and biochemically “preprocess” the plant materials and in this way may facilitate the further utilization by termites.

THE ECOSYSTEM PERSPECTIVE

Dung deposited naturally on the soil surface by mammalian herbivores needs to be broken down and eventually incorporated into the soil layer as part of nutrient cycling. It was suggested some time ago (e.g. Adamson, 1943) that termites have an important role in maintaining the fertility of tropical soils and the productivity of ecosystems. In addition, termites promote aeration, drainage and penetration of roots, as well as contribute to pedoturbation via their epigeal lifestyle, accelerate the formation of humus and the cycling of mineral elements by consuming dead wood and other plant remains (Adamson, 1943). The question arises, whether the comminution of mammalian dung by termites is not only of autecological importance but also affects the functioning of the ecosystem, i.e. nutrient cycling, and if so how these effects may be described and quantified.

TABLE 1. Dung removal rates of termites measured in field experiments. Standardized removal rates were computed assuming a linear removal-time relation as e.g. found by Coe (1970). Abbreviations: d – days, m – months.

Original removal rate	System	Standardized removal rate (% dung removed/month)	Reference
100% / 80–85 d	savanna, Kenya dry season elephant dung <i>Odontotermes</i> sp. <i>Microtermes</i> sp.	ca. 36 %/m	Coe, 1977
80–85% / 5–9 m	pasture, Costa Rica dry + wet season cattle dung <i>Amitermes beaumontii</i> <i>Hoplotermes</i> sp. n.	ca. 12 %/m	Herrick & Lal, 1996
80% / 42 d (dry) 50% / 42 d (wet)	derived savanna, Nigeria dry + wet season cattle dung unknown termite sp.	ca. 57 %/m (dry) ca. 36 %/m (wet)	Omaliko, 1981
92% / 3 m	sorghum field, Burkina Faso wet season cattle dung <i>Macrotermes</i> sp. <i>Trinervitermes</i> sp.	ca. 31 %/m	Ouédraogo et al., 2004
42.2% / 3 ½ m	Chihuahuan desert, USA cattle dung <i>Gnathamitermes tubiformans</i> <i>Amitermes wheeleri</i>	ca. 12 %/m	Whitford et al., 1982

Removal rates

The results of five studies reporting the dung removal rates of termites in the field are summarized in Table 1. Since the removal rates, as reported in the original publications, were measured over different time intervals, we standardized them to: % dung removed/month. The five studies report that termites removed between 12–57% of available dung within one month. Overall, higher removal rates were measured in the dry than in the wet season (Coe, 1977; Omaliko, 1981; Whitford et al., 1982; Ouédraogo et al., 2004). Removal rates were 12% / month for a desert, 36–57% / month in savannas, 31% / month in an agricultural field and 12% / month in a pasture. Despite the low sample size, savannas tend to have the highest removal rates. Over all, the average dung removal rate by termites in these field studies was around 30% per month.

Preferences and seasonality

Another important aspect is the occurrence of food preferences and the different roles, of termites and dung beetles. The quantitative results shown in Table 1 also reflect a general qualitative trend: higher removal rates are found during the dry season in each habitat. As mentioned earlier, Ferrar & Watson (1970) also concluded that termites prefer dry dung pats. A single study (Herrick & Lal, 1996) documents an increased comminution of cattle dung by *Amitermes beaumontii* and *Hoplotermes* sp. n. in a Neotropical pasture ecosystem in the wet season. Many authors, e.g. Weir (1971), report that dung beetles are responsible for the removal and burial of almost all dung during the wet season. This has led various authors to state that dung beetles are generally responsible for

nutrient recycling from dung (e.g. Losey & Vaughan, 2006). It appears that this is, however, only true for the wet season: since adult dung beetles feed exclusively on the liquid component of the dung by means of specialized filtering mouthparts (Holter, 2000), they rely on the availability of dung with a high water content. In addition, some dung beetle species (e.g. *Onthophagus binodis*) produce significantly fewer brood balls when the soil is dry (Barkhouse & Ridsdill-Smith, 1986). This means that in the dry season termites seem to gain in importance relative to dung beetles. But dung is not only temporally but also spatially a very heterogeneous resource; it is not permanently available to termites, because of the mobile lifestyle of its producers, while termites are sessile and bound to their nests. In contrast dung beetles are mobile and able to follow the producers. These factors might account for the food-preferences (dung vs. other natural items) of termites (Table 2). Overall, termites show no clear, distinct preference for mammalian dung over other plant food items.

A very interesting pattern is revealed if the 12 fungus-growing taxa (Macrotermitinae) are compared with the remaining ten species that do not grow fungi: while half of the Macrotermitinae taxa show a preference for alternative plant food items (50%), or no clear preference at all (33%), the greater part (70%) of the non-fungus-growers prefer dung (Table 2). The finding regarding the fungus-growers is surprising, given the apparent advantageous nutritional characteristics of dung. Feeding on mammalian dung, however, might be even disadvantageous to a certain extent for termites, especially the Macrotermitinae: about 330 termite species in this sub-

TABLE 2. Food preferences of termites with respect to the consumption of mammalian dung. Abbreviations: ca – cattle dung, el – elephant dung, ho – horse dung, to – tortoise droppings, M – measurement taken.

Food preference	Species	Reference
grass = ground wood > el dung el dung = grass el dung = grass = ground wood > “other” dung el dung = grass = ground wood > ”other” dung ground wood > el dung ground wood > el dung	<i>Macrotermes subhyalinus</i> <i>Odontotermes badius</i> <i>Odontotermes zambesiensis</i> <i>Odontotermes mediocris</i> <i>Microtermes allaudanus</i> <i>Synacanthotermes zanzibarensis</i>	Buxton, 1981 M: semi-quantitative (minor vs. major consumption)
el dung > litter	<i>Odontotermes</i> sp. <i>Microtermes</i> sp.	Coe, 1977 M: No. plots with termites
woody litter > mammalian dung	<i>Macrotermes michaelsoni</i> <i>Microtermes</i> sp.	Dangerfield & Schuurman, 2000 M: descriptive
cattle dung > mesquite wood	<i>Gnathamitermes tubiformans</i> <i>Amitermes wheeleri</i>	Ettershank et al., 1980 M: No. termite attack holes
cattle dung > control (litter etc.)	<i>Amitermes beaumonti</i> <i>Hoplotermes</i> sp. n.	Gould et al., 2001 M: individuals/plot
cattle dung > control (litter etc.)	<i>Amitermes beaumonti</i> <i>Hoplotermes</i> sp. n.	Herrick & Lal, 1996 M: termites/l of soil
cattle dung > litter <i>Yucca</i> wood > litter	unknown	Johnson & Whitford, 1975 M: foraging groups/source/ha
<i>Andropogon</i> or maize straw > cattle dung	<i>Macrotermes</i> sp. <i>Trinervitermes</i> sp.	Ouédraogo, 2004 M: individuals/bait
millet (canes or ground) > cattle manure millet (canes) > manure > ground millet	<i>Macrotermes subhyalinus</i> <i>Odontotermes nilensis</i>	Rouland et al., 2003 M: mass of soil sheeting
litter (Restionaceae) > ca,el,ho,to dung	<i>Amitermes hastatus</i>	Skaife, 1955 M: descriptive (lab)

family are known to cultivate a specialized fungus, genus *Termitomyces*, for food (Mueller et al., 2005). The nest of a single termite species can have different, but a few, symbiotic species (Aanen et al., 2002). Since termite nests provide conditions (high humidity, stable temperature) that favour microbial growth (Roy et al., 2006), termite nests also are favourable habitats for entomopathogenic fungi and bacteria, which hypothetically could be present in herbivore dung. Social insects are known to show host-mediated behaviour such as increased grooming, increased nest cleaning, secretion of antibiotics, dispersal of infected individuals and relocation of the entire colony in order to reduce pathogen transmission (Roy et al., 2006). The finding that fungus-growing termites do not prefer herbivore dung might be a way of avoiding pathogens. From the fungal symbionts' perspective, it may be more beneficial that termites feed it the same type of organic matter (e.g. a dominant grass) throughout the year, rather than vary greatly the type of food. It is possible, that termites exploit mammalian dung opportunistically if it becomes available as a food source, but the spatial and temporal heterogeneity of the availability of this food source counteracted the evolutionary development of a distinct behavioural preference for this food source, at least in some groups of termites.

Impacts on nutrient cycling

Despite the lack of evidence that termites as a whole prefer to feed on dung, there is support for the concept

that the comminution of mammalian dung by termites affects the ecosystem functioning via nutrient cycling.

Coe (1977) estimates that in the Tsavo (East) National Park (Kenya) termites remove up to 8.7×10^3 kg faeces per km² per year from the surface of the soil. This results in a nitrogen turnover of about 12 kg/ha/year based on the nitrogen content of 1.39% for fresh elephant dung reported by Anderson & Coe (1974). This gives a quantitative measure of the role of termites in facilitating the return of nutrients to the soil after they have passed through the primary consumer (mammalian herbivores) in the nutrient cycle. Without a directly comparable estimate of the removal of dung by dung beetles, the overall, quantitative importance of this process remains elusive. Herrick & Lal (1996) studied dung removal by termites associated with the transport of soil, both within the soil profile and to the soil surface (pedoturbation). They found a strong linear relationship between dung removal and soil accumulation at the original soil surface, with an average of 2.0 g of soil accumulated for every gram of dung that is removed. For their Neotropical pasture system, they give a minimum estimate of 2450 kg ha⁻¹ year⁻¹ of soil turnover in association with dung produced by two animal units ha⁻¹ (Herrick & Lal, 1996). Basappa & Rajagopal (1990) examined the physical and chemical properties of termite modified soils in India. This revealed that the water holding capacity, pH, organic carbon, organic matter, total nitrogen, the cation exchange capacity, as well as the exchangeable cations, like calcium, magne-

sium, potassium and sodium, were higher in termite modified soils than in surrounding soils (Basappa & Rajagopal, 1990). Some of these findings (e.g. regarding phosphorous) may be explained by the incorporation of organic matter and left-over dung into termite modified soil. Similar findings are also to be expected for non-dung feeding termites. Independent of the actual source of nutrients or the processes underlying the enrichment, termite modified soils are richer in nutrients; nutrients that in turn may enhance primary productivity. This second process may be temporarily delayed: Weir (1971) used radioactive P_{32} to study the removal of dung by termites in Zimbabwe. This author documented that termites (unknown species) consume dung, but no radioactivity was detected in the adjacent vegetation during the five months of the dry season when the measurements were made. Thus, the removal of nutrients by termites to their mounds did not result in this material becoming accessible to plants during the dry season (Weir, 1971). This event might be delayed until a termite colony dies and the mound or nest is eventually subject to erosion; e.g. shown by Coventry et al. (1988).

Furthermore, studies document that the consumption of mammalian dung influences the spatial distribution of termites. Gould et al. (2001) found *Amitermes beaumonti* to be more abundant in the stratum ranging from 0–3.5 cm below the cattle dung baits they used in Costa Rica (vs. the 3.5–7.0 cm stratum). Exactly the opposite pattern was found in control areas, indicating that at least this termite species adjusts its subterranean foraging behaviour according to the accessibility of dung. From the mammalian perspective, Coe & Carr (1978) report that blesboks (*Damaliscus dorcas phillipsi*) appear to deliberately place their middens in the vicinity of mounds of harvester termites (*Trinervitermes trinervoides*). They hypothesize that this is due either to the fact that termite mounds provide a spot of bare ground and therefore increased visibility for detecting predators and/or that blesboks are attracted to the mounds due to the increased foraging quality of the surrounding vegetation. The latter reasoning indicates this could constitute a positive feedback loop involving foraging behaviour of termites and mammalian herbivores, but this needs further clarification.

With respect to the overall nutrient cycling, termites may be seen as the crucial connective component between the dung producing herbivores and microbial decomposers in savannas by further fragmenting, and maybe even more important, spatially redistributing the dung particles. From temperate regions it is known that invertebrates, such as earthworms, are of critical importance: they comminute and ingest the plant debris, resulting in the incorporation of organic matter into the soil, as well as significantly increasing its surface area, but changing it little chemically (Burgess, 1967). If herbivore dung is regarded as partially decomposed plant material, it becomes apparent that termites and earthworms fulfil comparable ecological roles in these ecosystem dynamics. The major difference between termites and other invertebrate decomposers is that, especially in savannas, consid-

erable quantities of plant materials are consumed by wood-, grass- and fresh litter-feeding termites before and not after it has been attacked by saprophytic microorganisms (Wood, 1976). In the case of herbivore dung, this distinction does not hold anymore, since the plant material already has been attacked by the herbivores' own gut-endosymbionts. In contrast to the equivalent feeding guild of earthworms in temperate regions though, mound-building, fungus-growing termites (e.g. *Macrotermes*) are capable of engineering their own soil microclimate in order to facilitate the decomposition of plant materials by their symbiotic fungi.

CONCLUDING REMARKS

From an autecological point of view, we found a previously underestimated diversity of termite taxa feeding on a wide range of mammalian dung.

From the ecosystem perspective, we conclude that termites remove substantial quantities of mammalian dung and associated soil, over a relatively short period mainly in the dry season. The foraging on dung appears to be of only opportunistic importance to termites. No distinctive preference for mammalian dung could be detected for termites as a whole and for fungus-growers in particular, but was found for non-fungus-growing termites. By removing large quantities of dung from above to below the soil surface, by being responsible for substantial pedoturbation and nutrient enrichment of soils as well as by causing changes in the spatial distribution of termites and even the mammalian dung producers themselves, this feeding behaviour appears to be of great importance at the ecosystem level.

Coming back to our initial question whether termites, by foraging on mammalian dung, might fulfil a comparable ecological role to dung beetles in the context of nutrient cycling, we conclude that the current body of literature supports qualitatively the view that these two feeding guilds are both of ecological significance, but insufficient, quantitative information exists to definitely answer this question at this point in time.

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APPENDIX. Termites reported to forage on dung. Dung consumed: br – black rhinoceros, bu – buffalo, ca – cattle, cam – camel, di – dikdik, do – donkey, el – elephant, em – emu, go – goat, ho – horse, hy – hyrax, im – impala, ku – kudu, kw – kangaroo/wallaby, sh – sheep, sm – small buck, sp – springbok, to – tortoise, wo – wombat, ze – zebra; Country: Au – Australia, BF – Burkina Faso, Bo – Botswana, Br – Brazil, CR – Costa Rica, In – India, Ke – Kenya, Na – Namibia, SA – South Africa, Se – Senegal, Tz – Tanzania, USA, Zi – Zimbabwe; Habitat: AF – agricultural field, Bu – bush land/wood land, De – desert, Pa – pasture, Sa – savanna; Study: Ex – experiment in field, La – laboratory, Su – survey; Other diet: W – wood-feeding, L – litter-feeding, S – soil-feeding.

Taxon	Dung	Country	Habitat	Study	Other diet	Reference
MASTOTERMITIDAE						
<i>Mastotermes darwiniensis</i>	ca	Au	?	Su	WL	Ferrari & Watson, 1970; Gay & Calaby, 1970
RHINOTERMITIDAE						
<i>Heterotermes cf. tenuis</i>	ca	Br	Sa	Ex	W	DeSouza, 1993
<i>Heterotermes ferox</i>	ca,ho	Au	?	Su	W	Ferrari & Watson, 1970
<i>Heterotermes longiceps</i>	ca	Br	Sa	Ex	W	DeSouza, 1993
<i>Heterotermes paradoxus</i>	ca,ho	Au	?	Su	W	Ferrari & Watson, 1970
<i>Psammotermes allocerus</i>	br,ca, cam,do,el, go,ho,sh,sp,ze	Na Zi	Bu,Sa Bu	Su Su	W W	Coaton & Sheasby, 1972 Mitchell, 1980
<i>Psammotermes hybostoma</i>	?	?	?	?	?	Harris, 1970
<i>Schedorhinotermes actuosus</i>	ca	Au	?	Su	WL	Ferrari & Watson, 1970
<i>Schedorhinotermes seclusus</i>	ho	Au	?	Su	W	Ferrari & Watson, 1970
TERMITIDAE						
Apicotermitinae						
<i>Anoplotermes</i> spp. a,b	ca	Br	Sa	Ex	S	DeSouza, 1993
<i>Grigiotermes</i> sp.	ca	Br	Sa	Ex	S	DeSouza, 1993
<i>Hoplotermes</i> sp. n.	ca	CR	Pa	Ex	?	Herrick & Lal, 1996; Gould et al., 2001
<i>Ruptitermes</i> spp. a,d	ca	Br	Sa	Ex	S	DeSouza, 1993
Macrotermitinae						
<i>Allodontermes</i> sp.	ca,do, el,ho,ku,ze	Na Zi	Bu,Sa Bu,Sa	Su Su	WL WL	Coaton & Sheasby, 1972 Mitchell, 1980
<i>Ancistrotermes latinotus</i>	ca,el, ku,sm	Zi SA	Bu,Sa Bu,Sa	Su Su	WL WL	Mitchell, 1980 Uys, 2002
<i>Macrotermes</i> sp.	ca,el	Na	Bu,Sa	Su	WL	Coaton & Sheasby, 1972
<i>Macrotermes</i> sp.	ca	BF	AF	Ex	WL	Ouédraogo et al., 2004
<i>Macrotermes falciger</i>	ca,el	Zi	Bu,Sa	Su	WL	Mitchell, 1980
<i>Macrotermes michaelsoni</i>	ca,el	Bo,Zi	Bu,Sa	Su	WL	Dangerfield & Schuurman, 2000; Mitchell, 1980
<i>Macrotermes subhyalinus</i>	ca,el	Ke,Zi	Bu,Sa	Su	WL	Buxton, 1981; Mitchell, 1980
<i>Macrotermes subhyalinus</i>	ca	Se	Sa	Ex	WL	Rouland et al., 2003
<i>Macrotermes ukuzii</i>	bu,cal,	Zi	Bu,Sa	Su	WL	Mitchell, 1980
<i>Microtermes</i> sp.	bu,ca,do, el,ho, ku,sh	Na Ke Bo	Bu,Sa Bu,Sa Bu,Sa	Su Ex Su	W W W	Coaton & Sheasby, 1972 Coe, 1977 Dangerfield & Schuurman, 2000
<i>Microtermes allaudanus</i>	el	Ke	Bu,Sa	Su	W	Mitchell, 1980
<i>Odontotermes</i> sp.	ca,do,	Na	Bu,Sa	Su	W	Buxton, 1981 Coaton & Sheasby, 1972

	el,ho,ku,ze	Ke	Bu,Sa	Ex	W	Coe, 1977
<i>Odontotermes amaniensis</i>	?	Ke	?	Ex	W	Burchard, 1989
<i>Odontotermes badius</i>	ca,el	Ke,Zi	Bu,Sa	Su	WL/L	Buxton, 1981; Mitchell, 1980
<i>Odontotermes boranicus</i>	el	Tz	Bu	Su	W	Kemp, 1955
<i>Odontotermes horni</i>	?	In	?	Ex	?	Basappa & Rajagopal, 1990
<i>Odontotermes latericius</i>	ca,el	Zi	Bu,Sa	Su	W	Mitchell, 1980
<i>Odontotermes mediocris</i>	el	Ke	Bu,Sa	Su	WL	Buxton, 1981
<i>Odontotermes nilensis</i>	ca	Se	Sa	Ex	WL	Rouland et al., 2003
<i>Odontotermes obesus</i>	?	In	?	Ex	?	Basappa & Rajagopal, 1990
<i>Odontotermes patruus</i>	ca	Tz	Bu	Su	W	Kemp, 1955
<i>Odontotermes stercorivorus</i>	?	Ke	?	Ex	W	Burchard, 1989
<i>Odontotermes transvaalensis</i>	ca	Zi	Bu,Sa	Su	W	Mitchell, 1980
<i>Odontotermes wallonensis</i>	?	In	?	Ex	?	Basappa & Rajagopal, 1990
<i>Odontotermes zambesiensis</i>	el	Ke	Bu,Sa	Su	WL	Buxton, 1981
<i>Pseudacanthotermes militaris</i>	ca	Zi	Bu	Su	WL	Mitchell, 1980
		SA		Su		Uys, 2002
<i>Synacanthotermes zanzibarensis</i>	el	Ke	Bu,Sa	Su	W	Buxton, 1981
Nasutitermitinae						
<i>Armitermes</i> spp. a,b,c	ca	Br	Sa	Ex	S	DeSouza, 1993
<i>Atlantitermes stercophilus</i>	ca	Br	Sa	Ex	S	Constantino & DeSouza, 1997
<i>Baicalitermes hainesi</i>	ca	Na	Bu,De,Sa	Su	L	Coaton & Sheasby, 1972
<i>Cornitermes</i> sp.	ca	Br	Sa	Ex	W	DeSouza, 1993
<i>Diversitermes diversimilis</i>	ca	Br	Sa	Ex	W	DeSouza, 1993
<i>Embiratermes heterotypus</i>	ca	Br	Sa	Ex	S	DeSouza, 1993
<i>Embiratermes spissus</i>	ca	Br	Sa	Ex	S	DeSouza, 1993
<i>Fullitermes coatoni</i>	ca	Zi	Bu,Sa	Su	WL	Mitchell, 1980
		SA		Su		Uys, 2002
<i>Labiatermes</i> spp. a,b	ca	Br	Sa	Ex	S	DeSouza, 1993
<i>Nasutitermes coxipoensis</i>	ca	Br	Sa	Ex	W	DeSouza, 1993
<i>Nasutitermes eucalypti</i>	ca	Au	?	Su	W	Ferrar & Watson, 1970
<i>Nasutitermes kemneri</i>	ca	Br	Sa	Ex	W	DeSouza, 1993
<i>Nasutitermes kimberleyensis</i>	ca	Au	?	Su	W	Ferrar & Watson, 1970
<i>Nasutitermes longipennis</i>	ca	Au	?	Su	WL	Ferrar & Watson, 1970
<i>Nasutitermes torresi</i>	ca,ho	Au	?	Su	?	Ferrar & Watson, 1970
<i>Paracornitermes laticephalus</i>	ca	Br	Sa	Ex	S	DeSouza, 1993
<i>Procornitermes</i> sp.	?	?	?	?	?	Araujo, 1970
<i>Procornitermes</i> sp.	ca	Br	Sa	Ex	S	DeSouza, 1993
<i>Rhadinotermes coarctatus</i>	ca	Zi	Bu,Sa	Su	WL	Mitchell, 1980
<i>Rhynchotermes nasutissimus</i>	ca	Br	Sa	Ex	L	DeSouza, 1993
<i>Rhynchotermes</i> sp. a						
<i>Subulitermes</i> sp.	ca	Br	Sa	Ex	S	DeSouza, 1993
<i>Syntermes</i> sp.	ca	Br	Sa	Ex	L	DeSouza, 1993
<i>Trinervitermes</i> sp.	ca,el,ho	Na	Bu,Sa	Su	L	Coaton & Sheasby, 1972
	ca	Zi	Bu,Sa	Su	L	Mitchell, 1980
	ca	BF	AF	Ex	L	Ouédraogo et al., 2004
<i>Tumulitermes comatus</i>	ca	Au	?	Su	WL	Ferrar & Watson, 1970
<i>Tumulitermes dalbiensis</i>	ho	Au	?	Su	L	Ferrar & Watson, 1970
<i>Velocitermes paucipilis</i>	ca	Br	Sa	Ex	L	DeSouza, 1993
<i>Velocitermes</i> spp. 1,2,g	ca	Br	Sa	Ex	L	DeSouza, 1993
Termitinae						
<i>Amitermes</i> sp.	br,ca,	Na	Bu,Sa	Su	W	Coaton & Sheasby, 1972
	do,el,go,ho,sh,ze	Au	?	?	?	Gay & Calaby, 1970
<i>Amitermes abruptus</i>	ca,ho,kw,sh	Au	?	Su	WL	Ferrar & Watson, 1970
<i>Amitermes agrilus</i>	ca	Au	?	Su	WL	Ferrar & Watson, 1970
<i>Amitermes beaumonti</i>	ca	CR	Pa	Ex	?	Herrick & Lal, 1996; Gould et al., 2001
<i>Amitermes boreus</i>	ca,ho	Au	?	Su	WL	Ferrar & Watson, 1970

<i>Amitermes capito</i>	ca	Au	?	Su	W	Ferrar & Watson, 1970
<i>Amitermes colonus</i>	ho,sh	Au	?	Su	W	Ferrar & Watson, 1970
<i>Amitermes darwini</i>	ca,ho,sh	Au	?	Su	WL	Ferrar & Watson, 1970
<i>Amitermes dentosus</i>	ca,ho,sh	Au	?	Su	W	Ferrar & Watson, 1970
<i>Amitermes deplenus</i>	ho	Au	?	Su	W	Ferrar & Watson, 1970
<i>Amitermes eucalypti</i>	ca	Au	?	Su	W	Ferrar & Watson, 1970
<i>Amitermes exilis</i>	ca,ho	Au	?	Su	W	Ferrar & Watson, 1970
<i>Amitermes germanus</i>	ca,ho	Au	?	Su	W	Ferrar & Watson, 1970
<i>Amitermes gracilis</i>	ca	Au	?	Su	?	Ferrar & Watson, 1970
<i>Amitermes hartmeyer</i>	ca,ho,kw	Au	?	Su	W	Ferrar & Watson, 1970
<i>Amitermes hastatus</i>	ca,el,ho,to	SA	Bu,Sa	La	L	Skaife, 1955
<i>Amitermes herbertensis</i>	ca	Au	?	Su	W	Ferrar & Watson, 1970
<i>Amitermes heterognathus</i>	ca	Au	?	Su	WL	Ferrar & Watson, 1970
<i>Amitermes lanceolatus</i>	ca,ho	Au	?	Su	W	Ferrar & Watson, 1970
<i>Amitermes latidens</i>	ca	Au	?	Su	W	Ferrar & Watson, 1970
<i>Amitermes lativentris</i>	ca,ho	Au	?	Su	WL	Ferrar & Watson, 1970
<i>Amitermes laurensis</i>	ca	Au	?	Su	L	Ferrar & Watson, 1970
<i>Amitermes modicus</i>	ca	Au	?	Su	WL	Ferrar & Watson, 1970
<i>Amitermes neogermanus</i>	cam,ca,ho	Au	?	Su	WL	Ferrar & Watson, 1970
<i>Amitermes obtusidens</i>	ca,ho	Au	?	Su	W	Ferrar & Watson, 1970
<i>Amitermes perarmatus</i>	ca,em	Au	?	Su	WL	Ferrar & Watson, 1970
<i>Amitermes sciangallorum</i>	el	Ke	Bu,Sa	Su	?	Buxton, 1981
<i>Amitermes vitiosus</i>	ca,ho	Au	?	Su	WL	Ferrar & Watson, 1970
<i>Amitermes westraliensis</i>	ca	Au	?	Su	WL	Ferrar & Watson, 1970
<i>Amitermes wheeleri</i>	ca	USA	De	Ex	W	Ettershank et al., 1980 Whitford et al., 1982
<i>Amitermes xylophagus</i>	wo	Au	?	Su	W	Ferrar & Watson, 1970
<i>Amitermes</i> spp. I–V	ca	Au	?	Su	L	Ferrar & Watson, 1970
<i>Angulitermes</i> sp.	ca,el,ho,sh	Na	Sa	Su	WL	Coaton & Sheasby, 1972
<i>Angulitermes truncatus</i>	di	Tz	Bu	Su	L	Kemp, 1955
<i>Anoplotermes</i> sp.	?	?	?	?	?	Weesner, 1970
<i>Cubitermes</i> sp.	ca,el,im,ze	Na	Bu,Sa	Su	S	Coaton & Sheasby, 1972
<i>Eremotermes</i> sp.	?	?	?	?	?	Roonwal, 1970
<i>Gnathamitermes tubiformans</i>	ca	USA	De	Ex	L	Ettershank et al., 1980; Whitford et al., 1982
<i>Lepidotermes</i> sp.	ca,el	Na	Bu,Sa	Su	S	Coaton & Sheasby, 1972
<i>Microcerotermes</i> sp.	bu,ca,do, el,ho, hy,ze	Na,Tz,Zi	Bu,Sa	Su	W	Coaton & Sheasby, 1972 Kemp, 1955 Mitchell, 1980
<i>Microcerotermes cavus</i>	ca	Au	?	Su	W	Ferrar & Watson, 1970
<i>Microcerotermes distinctus</i>	ca	Au	?	Su	W	Ferrar & Watson, 1970
<i>Microcerotermes nervosus</i>	ca	Au	?	Su	W	Ferrar & Watson, 1970
<i>Microcerotermes serratus</i>	ca,ho	Au	?	Su	W	Ferrar & Watson, 1970
<i>Neocapritermes</i> sp.	?	?	?	?	?	Araujo, 1970
<i>Neocapritermes</i> spp. a,b,c	ca	Br	Sa	Ex	S	DeSouza, 1993
<i>Neocapritermes araguaia</i>	ca	Br	Sa	Ex	S	DeSouza, 1993
<i>Promirotermes</i> sp.	ca,el,ze	Na	Bu,Sa	Su	W	Coaton & Sheasby, 1972
<i>Synhamitermes</i> sp.	?	?	?	?	?	Araujo, 1970
<i>Termes boultoni</i>	el	Zi	De	Su	W	Mitchell, 1980